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# Multiple mating and clutch size in invertebrate brooders versus pregnant vertebrates

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We summarize the genetic literature on polygamy rates and sire numbers per clutch in invertebrate animals that brood their offspring and then compare findings with analogous data previously compiled for vertebrate species displaying viviparity or other pregnancy-like syndromes. As deduced from molecular parentage analyses of several thousand broods from more than 100 “pregnant” species, invertebrate brooders had significantly higher mean incidences of multiple mating than pregnant vertebrates, a finding generally consistent with the postulate that clutch size constrains successful mate numbers in species with extended parental care. However, we uncovered no significant correlation in invertebrates between brood size and genetically deduced rates of multiple mating by the incubating sex. Instead, in embryo-gestating animals otherwise as different as mammals and mollusks, polygamy rates and histograms of successful mates per brooder proved to be strikingly similar. Most previous studies have sought to understand why gestating parents have so many mates and such high incidences of successful multiple mating; an alternative perspective based on logistical constraints turns the issue on its head by asking why mate numbers and polygamy rates are much lower than they theoretically could be, given the parentage-resolving power of molecular markers and the huge sizes of many invertebrate broods.

genetic parentage analysis | mating systems | multiple paternity | polyandry | polygyny

Ever since Darwin (1), natural historians have understood that ecological and life-history constraints (including finite time and energy for reproductive activities coupled with limited mate availabilities) should have important impacts on mating behaviors and thereby on the evolution of mating systems and the operation of sexual selection in sexually reproducing species (2–6). Especially for species in which a parent invests heavily in offspring by incubating its young, additional constraints on successful polygamy by members of the incubating sex should arise because of the finite brood space available for rearing embryos within or attached to the incubator’s body. Many invertebrate animals guard embryos on or near their bodies in ways that are quite analogous to how vertebrate animals with internal pregnancy gestate their young. Here we address the mating-system ramifications of embryo brooding by contrasting genetically deduced incidences of polygamy by invertebrate parents that tend huge clutches versus pregnant vertebrates that carry many fewer progeny per gestation.

There are several reasons to suspect that individuals who gestate large broods might have higher incidences of polygamy (more mates and/or higher frequencies of multiple mating) than parents that tend smaller broods. First, large broods provide more statistical and physical room for multiple paternity or maternity, all else being equal. Second, many direct or indirect benefits that an incubating parent might gain from multiple mating could be amplified by the additional full-sib cohorts (different patriline in a brood) that a larger brood in principle can accommodate. Third, because of greater potential fitness payoffs, members of the nongestating sex also should have higher incentives to mate preferentially with brooder individuals that

are more fecund (i.e., carry larger broods). For all these reasons, it might be expected that genetic parentage analyses would reveal that large-clutch individuals and large-clutch species average many more full-sib cohorts per litter than do their smaller-clutch counterparts. Thus, we were surprised to find that this expectation does not appear to be well met in the huge scientific literature on animal genetic mating systems.

This is the third of three papers dealing with possible relationships between clutch size (fecundity) and propensities for polygamy in species that have, in effect, various expressions of pregnancy. In the first article of this series (7), we compared incidences of multiple mating by members of the pregnant sex in fish species with three alternative gestational modes: internal female-pregnancy, internal male-pregnancy, and external male-pregnancy (nest-tending by sires). We uncovered only mild statistical trends consistent with the hypothesis that pregnancy truncates fecundity in ways that impact selective pressures on pregnant individuals’ propensities to seek multiple mates. In a second article (8), we extended this type of analysis to assess polygamy rates in viviparous mammals vis-à-vis pregnant fish species. Results led us to advance a logistical-constraint hypothesis suggesting that low mate-encounter rates routinely truncate rates of multiple mating far below levels that otherwise could be accommodated, especially in species with large broods. Here we extend such appraisals of pregnancy-like phenomena by comparing published rates of polygamy by the incubating parent in invertebrate animals versus vertebrate animals that gestate their clutches of young.

In all these studies we take advantage of the fact that mate numbers and rates of multiple mating are documented much more readily for members of the gestating sex than for members of the nongestating sex (9). For any category of pregnancy, multiple successful mating by the adult caregiver is relatively straightforward to detect in nature via genetic parentage analyses because each resulting brood of embryos is physically associated with its pregnant sire or pregnant dam. By contrast, documenting the incidences of polygamy by members of the nonpregnant sex is much more problematic, because each such individual may have parented additional broods that happened not to be included in the genetic assays. Taking advantage of this inherent sex-based asymmetry, researchers in recent decades have used highly polymorphic molecular markers (notably microsatellite loci) to estimate mate numbers and rates of multiple mating by the caregiving parent in a wide diversity of viviparous and other species that gestate or otherwise tend their brooded offspring. Here we compile this scientific literature for invertebrate brooders and compare the findings with those we previously summarized for vertebrate animals that display viviparity or other pregnancy-like phenomena.

Author contributions: J.C.A. designed research; A.T. and J.-X.L. performed research; A.T. and J.-X.L. analyzed data; and J.C.A. wrote the paper.

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**Table 1. Summary statistics of mating parameters of invertebrates**

Species	No. of clutches examined	Clutch size	% clutches with multiple paternity (actual numbers)	Mean no. of mates (range)	No. of alleles at most polymorphic marker (no. of marker loci)	Mode of offspring housing	Reference
Knobbed whelk, <i>Busycon carica</i>	12	Several thousand	92 (11/12)	3.5 (1–7)	36 (3)	Eggcase string	28
Slipper shell, <i>Crepidula fornicata</i>	6	Average 7,500	100 (6/6)	3.3 (2–5)	37 (4)	Give birth	11
Slipper shell, <i>Crepidula fornicata</i>	18	25,000	78 (14/18)	2.6 (1–5)	32 (5)	Give birth	12
Slipper shell, <i>Crepidula fornicata</i>	12	Average 7,500	92 (11/12)	2.8 (1–4)	45 (5)	Give birth	13
Slipper shell, <i>Crepidula coquimbensis</i>	5	Hundreds to thousands	100 (5/5)	4.4 (3–5)	18 (5)	Direct development	14
Sea hare, <i>Aplysia californica</i>	33	Hundred thousands to millions	76 (25/33)	2.1 (1–3)	23 (1)	Egg clutch	15
Land snail, <i>Anrianta arbustorum</i>	26	Dozens to hundreds	100 (26/26)	3.7 (2–6)	8 (4)	Egg mass, direct development	16
Flat periwinkle, <i>Littorina obtusata</i>	3	50–150	100 (3/3)	5.0 (4–6)	14 (3)	Egg mass, direct development	17
Rough periwinkle, <i>Littorina saxatilis</i>	4	23–302	100 (4/4)	19.3 (15–23)	23 (5)	Ovoviviparity	18
Calamary, <i>Sepioteuthis australis</i>	35	Hundred	97 (34/35)	2.7 (1–4)	14 (5)	Egg strand	19
Veined squid, <i>Loligo forbesi</i>	3	Hundred	67 (2/3)	1.7 (1, 2)	25 (6)	Egg string	20
Inshore squid, <i>Loligo pealeii</i>	5	Several thousand	100 (5/5)	3.0 (2–4)	34 (3)	Egg strand	21
Chokka squid, <i>Loligo vulgaris</i>	4	Several thousand	50 (2/4)	2.8 (1–5)	30 (4)	Egg string	22
Octopus, <i>Graneledone boreopacifica</i>	1	57	100	2.0 (2)	6 (18)	Egg string	23*
Snapping shrimp, <i>Alpheus angulosus</i>	54	Several hundred	22 (12/54)	1.2 (1, 2)	29 (5)	Extended maternal care	(24)
Ghost shrimp, <i>Callichirus islagraunde</i>	40	Several thousand	20 (8/40)	1.2 (1–3)	31 (2)	Extended maternal care	25
Freshwater shrimp, <i>Caridina ensifera</i>	20	16 (5–30)	100 (20/20)	5.3 (2–11)	25 (4)	Extended maternal care	26
Swamp crayfish, <i>Procambarus clarkii</i>	30	276 (136–362)	97 (29/30)	2.6 (1–4)	10 (4)	Extended maternal care	27
Placid crayfish, <i>Orconectes placidus</i>	15	250 (20–514)	60 (9/15)	1.8 (1–4)	22 (3)	Extended maternal care	10
Rugose squat lobster, <i>Munida rugosa</i>	25	Up to 30,000	84 (21/25)	2.2 (1–3)	14 (3)	Extended maternal care	29
Squat lobster, <i>Munida sarsi</i>	5	Up to 30,000	100 (5/5)	4.0 (4)	14 (2)	Extended maternal care	29
American lobster, <i>Homarus americanus</i>	108	Several thousand	13 (14/108)	1.2 (1–3)	24 (4)	Extended maternal care	30
Norway lobster, <i>Nephrops norvegicus</i>	11	140–4,000	55 (6/11)	1.1 (1–3)	37 (2)	Extended maternal care	31
Brown crab, <i>Cancer pagurus</i>	18	500,000–3 million	0 (0/18)	1.0 (1)	27 (3)	Extended maternal care	32
Porcelain crab, <i>Petrolisthes cinctipes</i>	10	1,300	80 (8/10)	1.9 (1–3)	47 (2)	Extended maternal care	33
Snow crab, <i>Chionoecetes opilio</i>	7	thousands	0 (0/7)	1.0 (1)	22 (2)	Extended maternal care	34
Praying mantis, <i>Ciulfina rentzi</i>	8	12 (10–14)	0 (0/8)	1.0 (1)	7 (2)	Ootheca	35
Praying mantis, <i>Ciulfina klassi</i>	7	12 (7–23)	57 (4/7)	2.1 (1–4)	9 (2)	Ootheca	35
Sea spider, <i>Ammothea hilgendorfi</i>	13	243 (35–774)	54 (7/13)	1.8 (1–3)	36 (4)	Paternal care	36
Sea spider, <i>Ammothella biunguiculata</i>	45	Dozens to hundreds	69 (31/45)	2.7 (1–9)	60 (5)	Paternal care	37
Ascidian, <i>Botryllus schlosseri</i>	14	NA	92 (13/14)	3.2 (1–5)	30 (4)	Viviparity	38 <sup>†</sup>

\*Not used in species analysis.

<sup>†</sup>Not used in brood analysis.

## Results

We uncovered published molecular appraisals of genetic parentage for a total of 583 broods of 29 invertebrate species (Table 1) plus 3,057 litters representing 93 vertebrate species in which either internal or external pregnancy is displayed either by females (the usual situation) or by males (7, 8). Table 2 summarizes and compares these findings for invertebrates versus vertebrates, as do Figs. 1 and 2 in graphical formats. As was true for the vertebrate litters, invertebrate broods routinely proved to be composed of several full-sib cohorts reflective of multiple successful mates for the gestating parent. Overall, slightly more than two-thirds of all surveyed invertebrate broods evidenced multiple mating, with the number of full-sib cohorts in a brood averaging  $2.19 \pm 0.08$  (SE) as calculated per brood or  $3.08 \pm 0.64$  as calculated per species (a calculation that, in effect, gives equal statistical weight to each species regardless of how many broods were assayed). All these summary statistics are significantly (or nearly so) higher than their vertebrate counterparts (Table 2). The record for the highest number of genetically deduced mates in any surveyed invertebrate brood was 23 [for one brood of the rough periwinkle, *Littorina saxatilis* (18)].

## Discussion

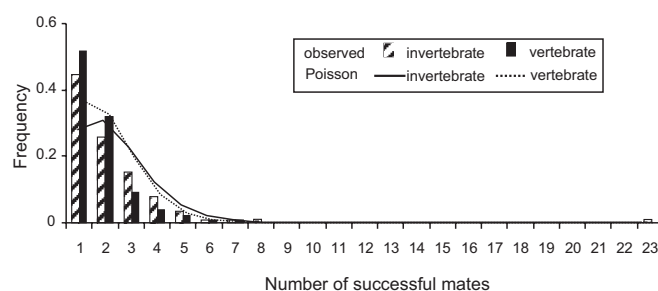
In many animal lineages, anisogamy (the larger size and lower motility of female gametes compared with male gametes) ultimately predisposed the evolution of female-pregnancy and maternal care of offspring, and these phenomena in turn can make females and their ova even more limiting as a reproductive resource. Thus, anisogamy set the evolutionary stage by making females more fecundity-limited than males, and gestational phenomena often amplify this sexual difference by placing further constraints on how many progeny a pregnant or brooding female can bear during her lifetime. In turn, these inherent fertility differences between the genders routinely translate into shallower sexual-selection gradients (39) for females than for males in many species, meaning that a male's reproductive success can increase greatly with higher mate counts, whereas a female's genetic fitness inherently is truncated by her limited fecundity, regardless of her particular mating behavior. Thus, conventional evolutionary wisdom holds that males often experience stronger selection pressures for multiple mating than do females, and this difference in sexual selection pressure is precisely why the relatively few species with male-pregnancy and/or sex-role reversal are of special evolutionary interest (36, 40).

**Table 2. Comparisons of mating parameters in invertebrate brooders versus pregnant vertebrates**

Mating-system parameter	Invertebrates (mean $\pm$ SE)	Vertebrates (mean $\pm$ SE)	<i>t</i> -statistic	df	<i>P</i> *	<i>P</i> <sup>†</sup>
No. of successful mates based on per-brood data	2.19 $\pm$ 0.08	1.77 $\pm$ 0.02	5.11	651	0.00	0.00
No. of successful mates based on per-species data	3.08 $\pm$ 0.64	1.88 $\pm$ 0.10	1.85	28	0.07	0.01
Proportion of broods with multiple mates based on per-species data	0.67 $\pm$ 0.07	0.51 $\pm$ 0.03	2.18	41	0.04	0.02

\*Two-tailed *t* tests assuming unequal variances.

<sup>†</sup>Results of a comparison by the Mann-Whitney *u* test.



**Fig. 1.** Frequency distributions of invertebrate and vertebrate broods in which gestators had the indicated numbers of successful mates (as deduced from genetic parentage analyses). Also shown are the relevant Poisson distributions (with same means as those that were observed) that have been truncated by apportioning the expected zero class (no mates) to the other mate classes.

Such species offer mirror-image vantages on animal mating systems and sexual selection.

Based in part on the logic introduced by Bateman (39), we take it almost as a given that members of the nonpregnant sex (usually males) tend to evolve behavioral dispositions to seek copulations with members of the pregnant sex (usually females). Thus, at issue here is not so much the mating behaviors by members of the nongestating sex but rather the mating proclivities of members of the gestating sex (exactly the issue that molecular parentage analyses are best suited to assess). Our current interest in comparing invertebrate brooders with pregnant vertebrates relates partly to the fact that incubator parents in these two groups often have very different clutch sizes (potential fecundities or fertilities). For example, most mammalian litters contain only a small handful of young, but many invertebrate broods number in the hundreds to many thousands of embryos (Table 1). Of course, vertebrate and invertebrate animals differ in countless biotic features that might influence mating decisions by members of the pregnant sex, so any observed difference in mating proclivities between these two groups might have nothing to do with brood size per se. On the other hand, if invertebrate brooders and pregnant vertebrates prove to have similar rates and patterns of polygamy despite their many biological differences, then such a finding itself might shed some light on the evolution of mating behaviors in species with high parental-investment tactics.

From our current survey of the literature on genetic parentage in "pregnant" animals, we have confirmed that most invertebrate broods consist of multiple full-sib cohorts, meaning that the gestating parent routinely must have had several successful mates. More than 50% of all surveyed invertebrate broods consisted of two or more such cohorts of embryos, and a typical brooding parent had about two to five successful sexual partners on average. These substantial rates of polygamy may not be surprising, given the several fitness rewards that in theory can attend polygamous mating behaviors by members of the gestating sex (Table 3). Rather, what we find surprising is that the overall mating profiles of invertebrate brooders are so remarkably similar to those of their vertebrate counterparts (Table 2 and Figs. 1 and 2).

When molecular markers were introduced to mating-system analyses in the latter part of the 20th century, many researchers were intrigued by what they interpreted as unexpectedly high rates of polygamy in many species otherwise suspected from field observations to be mostly monogamous (reviews in 9, 61). Thus, a research tradition arose wherein a primary goal was to explain why multiple mating by females (polyandry) was far more common than previously thought. Many hypotheses were advanced and tested in numerous taxa regarding possible direct and indirect fitness benefits that females might derive from polyandrous matings (Table 3). Of course, multiple mating was recognized to have potential downsides as well (such as the risk





gistical considerations should offer a helpful alternative perspective on animal mating systems, not least as a counterbalance to standard selectionist perspectives on polygamy. For the selection–neutrality debate in molecular evolution, the final resolution proved to be a compromise: Some loci are under selection, whereas others appear neutral or nearly so. With respect to the current issue of mate numbers in “pregnant” species, the final resolution undoubtedly will prove to be some balance between fitness payoffs of polygamous mating (Table 3) and the many limitations on multiple mating imposed by what is logistically feasible within each population (64).

## Materials and Methods

Our current literature review was conducted in the winter and spring of 2011. It sought to identify all substantive papers on rates of multiple paternity or multiple maternity for the assayed broods of gestating invertebrate species (most of which inhabit marine or freshwater environments), as estimated via

genetic parentage analyses that used highly polymorphic molecular markers. For each species, we summarize reported information on brood size, the proportion of broods with multiple sires (or multiple dams in the case of male-brooding species), successful numbers of mates for members of the brooding sex, and the resolving power of the particular polymorphic molecular markers that were used. Different authors sometimes used slightly different statistical procedures (see ref. 65) to quantify the incidence of multiple mating by the gestating sex, but in all cases we accepted the published estimates at face value.

For each relevant mating-system parameter (such as brood size and number of parents per brood), we calculated means and SEs and also performed regression analyses between variables. To compare the means of mating-system parameters in vertebrates versus invertebrates, we initially used *t* tests, but to accommodate nonnormality in the data we then verified the results with nonparametric Mann–Whitney *u* tests (66).

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